

other ("correlation" of $\log N$ with $\Delta \log N$) indicates density-disturbance (as defined by Nicholson 1954). Both cannot be right.

The method followed by Davidson and Andrewartha is clearly set out in their two papers and in Andrewartha and Birch (p. 587). We certainly did not, and we stated clearly that we did not, infer causal relationships from our regressions. On the contrary, our independent variates were chosen to represent causal relationships which we had inferred from a prior knowledge of the biology of *Thrips imaginis*. If we had overlooked a causal relationship, then, because the regression accounted for a high proportion of the variance, the neglected variable would, of necessity, be highly correlated with at least one of the variables included in the regression. From the nature of the variates that were included, it seems unlikely that a substitute could be found for any of them that would be consistent with the idea of "density-dependent factors."

We did not include an independent variate to represent a density-dependent factor because we could not find one. Our study of the biology of *T. imaginis* established, with reasonable certainty, that shortage of food was not operating as a density-dependent factor. We searched for evidence that predators, parasites or diseases were influential but failed to find it. Nor could we find any other component of environment that might be said to act like a density-dependent factor.

SUMMARY

Davidson and Andrewartha (1948b) concluded that the results of their study of a population of *Thrips imaginis*

provided no confirmation of the theory of density-dependent factors. Smith (1961) re-analyzed some of their results and reached the opposite conclusions. This paper suggests that Smith's conclusions are not acceptable because:

- (a) He made the logical error of inferring a causal relationship from a statistical correlation.
- (b) He made the statistical mistake of "correlating" two variables that were not ascertained independently.
- (c) He retained two criteria that gave opposite answers to the same question.

REFERENCES

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- Nicholson, A. J. 1954. An Outline of the Dynamics of Animal Populations, *Aust. J. Zool.* 2: 9-65.
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DENSITY-DEPENDENCE

FREDERICK E. SMITH

Department of Zoology, University of Michigan, Ann Arbor

In an effort, not to continue an argument, but to leave it as free of error as possible, the following comments are offered concerning the two papers on density-dependence in the Australian thrips:

(1) In the earlier paper (Smith 1961) a formula written $-\frac{1}{2}(s_a/s_b)$ should be $-\frac{1}{2}(s_b/s_a)$. This indicates the degree of negative correlation of population change with initial size that must exist if the population variance is to stay at its initial level.

(2) In the above reply population variance is said to increase from January, when it is 0.066, through August, when it is 0.043. Even the extremes of variation within this period, 0.024 in March and 0.137 in July, are not great enough to reach statistical significance, although the several ups and downs could certainly be discussed.

(3) In the above reply the positive correlation (0.85) between y_4 and y_5 is said to contribute to the negative correlation (-0.80) between $(y_5 - y_4)$ and y_4 . The actual situation is the reverse. If the first correlation were zero, the second would be -0.84 , and if the first were -0.85 , the second would be -0.98 . In equation (1) the third term in the denominator also occurs in the numerator.

(4) In the above reply the summer decrease in population variance is said to be due probably to the greater seasonal regularity of summer than of spring. In the absence of density-dependent mechanisms it is *mathematically* impossible for this situation as stated to reduce the

variance; it will merely lessen the rate of increase in variance. A decrease is possible if the weather in spring and summer are strongly inversely correlated, but this is not evident in published data.

(5) The negative correlations in the earlier papers are said to lack the necessary independence of measure to be "true." Admittedly they are biased. As stated in the earlier paper, using the estimates of sampling error that are published in the thrips study, the bias can be estimated and was found to be negligible. If, conversely, the observed correlations are considered to be due entirely to bias, then the great majority of variation in population size from one year to another would mathematically have to be due to sampling error, rather than reflecting "real" differences. If this is so the multiple regressions reported by Davidson and Andrewartha, 1948b in the above reply, will of mathematical necessity have to be considered spurious, since they also account for the great majority of variation in population size from one year to another.

(6) In the above reply two criteria are said to give conflicting results. It is incorrect, however, to infer positive correlations from variance increases. Of mathematical necessity the two criteria must vary concomitantly, although they do have different null points. Variance fails to increase only if *all* of the incoming variance is eliminated; correlation is negative if *any* of the incoming variance is eliminated. Equivalence between them is given in comment (1). The incorrect inference follows from the error discussed in comment (3).